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Species Migrations and Ecosystem Stability During Climate Change: The Belowground Connection

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Abstract: *Compatibility between the belowground mutualists of resident species and the needs of immigrant species will strongly influence the successful transition from one perennial plant community to another during climate change. A hiatus in the overlap between plant species that maintain a positive link with the soil ecosystem could result in site capture by weeds and rapid degradation of the productive capacity of soils. We discuss instances in which such rapid degradation has occurred and argue for the crucial importance of protecting plant-soil links in the coming decades through maintaining biodiversity and utilizing management practices that help plants keep a firm grip on the soil. Examples of the latter include partial and dispersed cutting in forestry, use of green cover crops in agriculture, and grazing intensities that permit degraded range to rebuild.*

Resumen: *La compatibilidad entre los mutualistas bajo el suelo de las especies residentes y las necesidades de las especies inmigrantes influenciará fuertemente la exitosa transición de una comunidad perenne a otra durante cambios climáticos. Una abertura en la superposición entre las especies de plantas que mantienen una relación positiva con el ecosistema del suelo podría resultar en la captura del lugar por yerbas y en la rápida degradación de la capacidad productiva de los suelos. Se discuten instancias en las que ha ocurrido esta rápida degradación y se argumenta la importancia crucial de proteger las cadenas de planta-suelo en las décadas venideras a través del mantenimiento de la biodiversidad y la utilización de prácticas de manejo que ayuden a las plantas a sostener un firme arraigo con el suelo. Ejemplos de lo último incluyen la tala parcial y dispersa en la silvicultura, el uso de cultivos con "cubierta verde" en la agricultura, y densidades de pastoreo que permitan la reconstrucción del rango degradado.*

Introduction

The ease with which plant species migrate northward and to higher elevations as climate changes will depend in part on compatibility between soils and the needs of incoming plants. Various aspects of soil chemistry, structure, and biology are likely to be involved. One factor of particular importance will be whether immigrants find

the mycorrhizal fungi and rhizosphere bacteria that they require. Another important factor is whether soil structure and nutrient content are maintained during the transition from one type to another. Both of these factors will depend either partly or wholly on the degree of overlap between outgoing plant species and immigrants that invest energy in soil structure and microbial mutualists. Insufficient overlap is likely to result in nutrient

loss and site capture by weeds — mobile opportunists that invest relatively little in soils.

Here we argue that protecting and nurturing the strong positive feedback links between plants and soils are of utmost importance if we are to avoid widespread ecosystem degradation in the coming years, and that preserving the stabilizing redundancies that result from plant-species diversity will be a key element in this task. We first briefly review what is known about compatibility among plant species with regard to belowground mutualists (mycorrhizae and rhizosphere bacteria) and speculate on how this might influence species migrations. We then turn to the question of ecosystem stability, presenting evidence from various ecosystems around the world that disruption of the self-reinforcing links between plants and soils can result and has resulted in rapid site degradation, and in at least some cases has led to virtual collapse of formerly productive ecosystems. We conclude that climate change, particularly when coupled with other stresses such as pollution, has the potential to break critical plant-soil links and lead to rapid site degradation that will be difficult and expensive to reverse. Strategies for preventing this are discussed. We stress that much research is needed on virtually all of the points discussed in this paper; our arguments should be considered as working hypotheses rather than established fact.

A Brief Review of the Plant-Soil Link

The belowground community is not distributed homogeneously within the soil volume but rather in islands of intense activity centered on energy sources. Although all forms of plant detritus can serve as an energy source, 90 percent or more of the microbes in soil are concentrated around living roots, mycorrhizae, and mycorrhizal hyphae (Richards 1987). Moreover, the species composition of the microbial community is quite different in the vicinity of roots and mycorrhizae than it is away from these zones. Energy allocated by plants to the belowground does work that benefits the plant, and plants and soils become closely linked through strong positive feedback (Perry et al. 1989a). Photosynthates flowing into the soil as exudates from roots and mycorrhizae — which may range from 10 percent to over 50 percent of net photosynthesis — support a diverse community of bacteria, fungi, and microinvertebrates. Many rhizosphere inhabitants reciprocate through one mechanism or another to positively influence plant growth (Fig. 1): gathering nutrients and water, fixing atmospheric nitrogen (in rhizospheres as well as nodules), protecting the plant host from pathogens, releasing various hormones and chelators, and modifying soil structure by binding small organomineral complexes into large (roughly > 0.25 mm) aggregates (reviews on one or another aspect

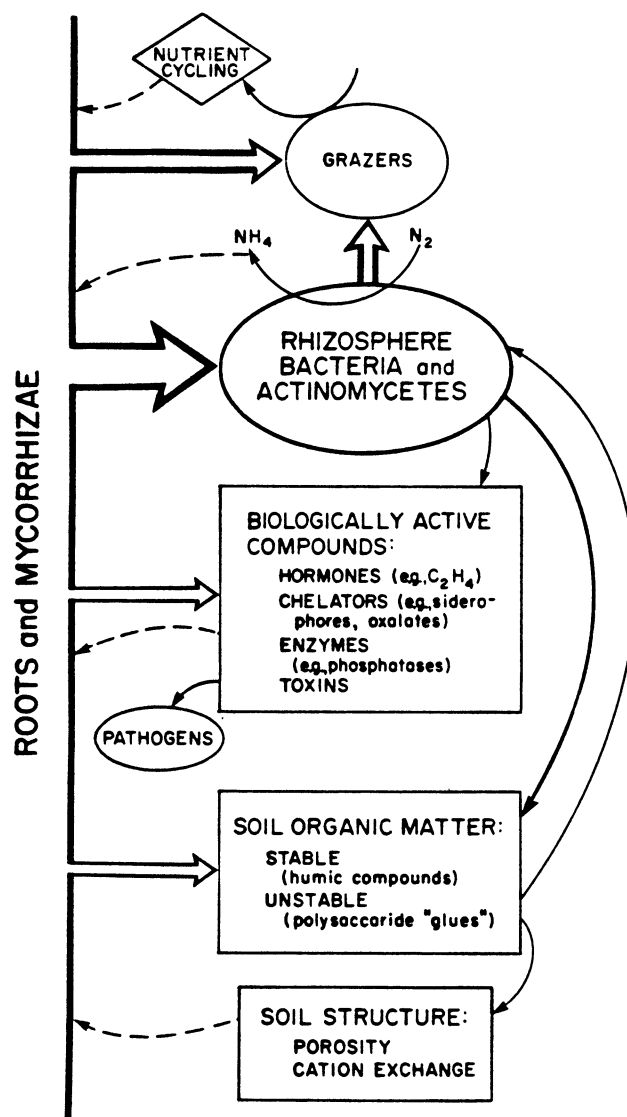


Figure 1. Schematic diagram of biotic processes within the mycorrhizosphere. Most energy exuded by mycorrhizae probably passes directly to bacteria; however, arrow widths do not necessarily reflect relative quantities of energy flow (Perry et al. 1987).

of rhizospheres include Rambelli 1973; Newman 1978, 1985; Bowen 1980; Schroth & Hancock 1982; Tisdall & Oades 1982; Coleman 1985; Linderman 1985; Lynch & Bragg 1985; Foster 1986; Whipps & Lynch 1986; Perry et al. 1987).

Of the soil microorganisms that benefit plants, most research has been devoted to two groups: mycorrhizal fungi and *Rhizobium* sp. (the nitrogen-fixing symbionts of legumes). We deal only with the former here. Between 80–90 percent of plant species form mycorrhizae, making it one of the most widespread and ecologically important symbioses in nature (reviews include Janos 1980; Malloch et al. 1980; St. John & Coleman 1982; Harley & Smith 1983). Conifers that have

been studied are always mycorrhizal in the wild. Of 6,507 species of angiosperms that have been studied, 70 percent are consistently found to be mycorrhizal and 12 percent are apparently facultatively mycorrhizal, sometimes forming mycorrhizae and sometimes not (Trappe 1987). A high proportion of plant species classified as the world's worst weeds (Holm et al. 1977) are facultatively mycorrhizal.

The most common mycorrhizal types are formed by two quite distinct groups of fungi. Ectomycorrhizae (EM), characterized by extensive hyphal development external to the root and by (usually) lack of penetration of host cells, are formed by several thousand species in the subdivisions Basidiomycotina and Ascomycotina. Vesicular-arbuscular (VAM), which penetrate host cells but do not modify the external appearance of the root, are formed by several hundred species in the family Endogonaceae, subdivision Zygomycotina. Trees and some shrubs are the predominant hosts of EM fungi, whereas a wide range of herbs, grasses, shrubs, and trees host VAM fungi. Some plants host both types.

We turn now to consider possible consequences if plant-soil links are disrupted during species migrations. This requires that we digress from a direct consideration of climate change to discuss examples in which sites have degraded rapidly under management. We will use these examples to argue for a new view of ecosystem stability that has significant implications for predicting ecosystem response to changing climate.

Threshold Degradation

Probably few ecologists would believe that threshold changes in ecosystem properties such as productive capacity can occur; for example, an old dictum of forest soil science states, "Once a forest soil, always a forest soil." Contrary to this dictum, considerable evidence suggests that threshold changes in ecosystem properties are not only possible, they are widespread. There are numerous examples throughout the world of apparently rapid and not-easily-reversible degradation of ecosystems including grasslands, high elevation temperate forests, and both moist and dry tropical forests (see the review by Perry et al. 1989b).

Our work on degradation has focused on the higher-elevation forests (roughly above 1,500 m) of southwest Oregon and northern California, where numerous clearcuts have remained unreforested for up to 25 years despite their having been planted on average four to five times each. We have intensively studied soil properties on one of these sites, Cedar Camp (Fig. 2). Logged in 1968, the clearcut at Cedar Camp is now dominated by an exotic annual grass (cheatgrass, *Bromus tectorum*), with scattered bracken fern clones and a few early successional shrubs that survived the herbicides used to "reduce competition" with planted tree seedlings. The



Figure 2. Cedar Camp, 20-year-old clearcut in the Siskiyou Mountains of southwest Oregon. This area has been planted four times, but all plantings have failed.

few tree seedlings that have established since logging occur adjacent to shrubs.

Cedar Camp was not marginal for tree growth prior to logging; forests adjacent to Cedar Camp are quite productive for that elevation (1,700 m), and growth rings on stumps show that the same was true of the forest that occupied the clearcut. As the fate of the clearcut demonstrates, however, the productive capacity of these sites is not due solely to inherent site properties; rather, it is a nonequilibrium phenomenon that is tied closely to trees and to the energy that trees invest in mycorrhizal fungi and other microbes, in soil structure, and in retaining and cycling nutrients. If logged and not quickly reforested, these sites degrade rapidly. Clearcut soils at Cedar Camp differ from those of the adjacent forest biologically and, because of the loss of certain biological components, structurally. Compared to the forest, clearcut soils have many more bacteria, fewer fungi, and four times as many actinomycetes (a common type of filamentous bacteria noted for producing biocides) that express allelopathy in bioassay (Perry & Rose 1983; Friedman et al. 1989). Concentrations of hydroxymate siderophores — microbially produced iron chelators that are important in plant nutrition and defense against pathogens — are also reduced in clearcut soils (Perry et al. 1984).

Some of the more striking changes at Cedar Camp are in soil structure. Figure 3 shows scanning electron micrographs of forest and clearcut soils. The granitic bedrock underlying this site forms sands that owe much of their structure to the binding action of roots and, especially, mycorrhizal hyphae such as those shown in the micrograph in Figure 4. Note that it is *living* roots and hyphae that structure these soils, not dead organic matter; total carbon differs little between forest and clearcut soils (J. G. Borchers & Perry 1989). Once these living components decay, soil structure degenerates.

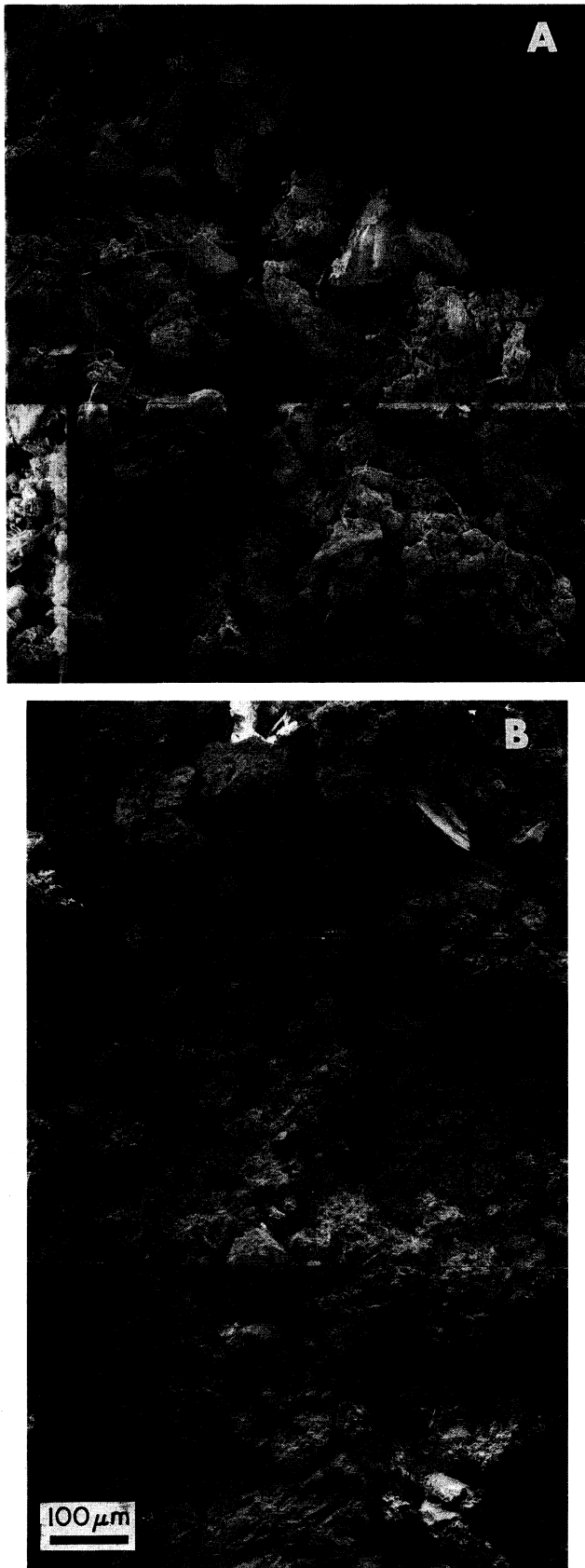


Figure 3. Scanning electron micrographs of soil from (A) a forest and (B) an adjacent unreforested clearcut of the Cedar Camp site, southwest Oregon (Perry et al. 1987).

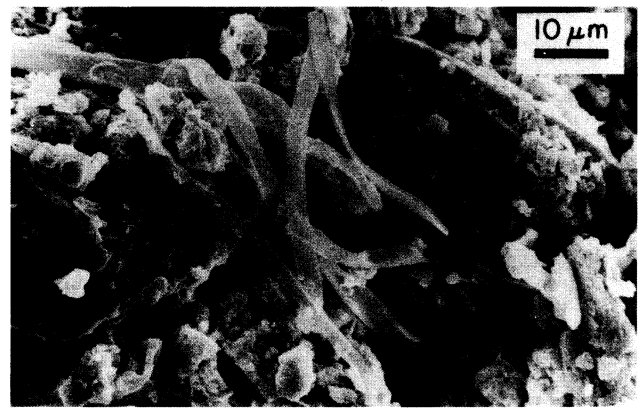


Figure 4. Scanning electron micrograph of fine-pore structure and hyphae in the forest soil of Figure 3 (hyphae collapsed during sample preparation) (Perry et al. 1987).

Cedar Camp was converted from a productive forest to an annual grassland within 20 years after trees were cut and sprouting hardwood shrubs herbicided. Early reforestation failures suggest that soils changed quite rapidly following clearcutting, but we cannot be sure of this. Our research indicates that trees can be reestablished at Cedar Camp if the right microbes are re inoculated. By adding 150 ml of soil from an established young forest to planting holes at the time of planting, we were able to get tree seedlings to survive and even thrive at Cedar Camp (Amaranthus & Perry 1987).

Is Cedar Camp a freak event, or does it indicate a more general type of system dynamic that is characterized by soil properties that are far from equilibrium and susceptible to threshold degradation? This question cannot be answered definitively without studying other sites, but we do not believe that Cedar Camp is an anomaly. At the very least, it probably represents many other unreforested clearcuts at high elevation throughout the western United States. Elsewhere we argue that the non-equilibrium dynamic exhibited by Cedar Camp also occurs in a wide variety of other ecosystems ranging from moist tropical forests through dry tropical forests to grasslands (Perry et al. 1989b).

Stability of Nonequilibrium Systems

The traditional view of system stability is that of classical physics — the system in equilibrium with its local environment (exemplified by a ball resting at the bottom of an energy well; Fig. 5a). However, a more appropriate metaphor for a nonequilibrium system such as an ecosystem is a ball balanced on a peak (Fig. 5b). The stability of a ball on a peak differs from that of a ball in a well in at least two important respects.

1. Whereas the probability of destabilizing the ball in the well (pushing it over the local hump into another well) is proportional to the applied force, de-

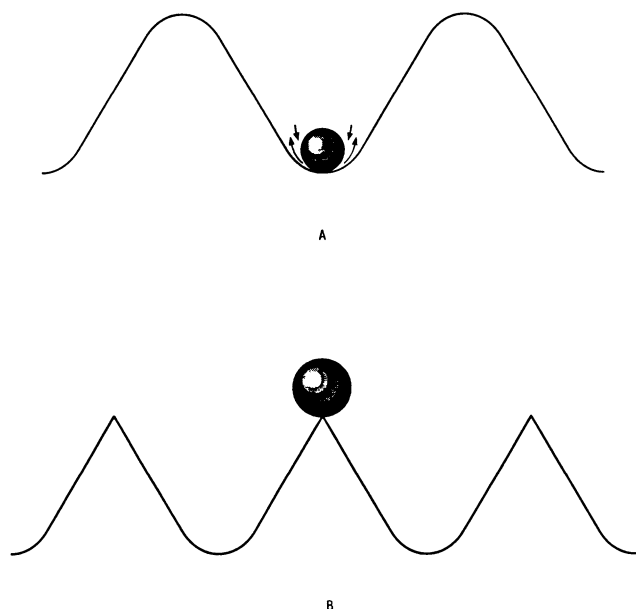


Figure 5. Two views of ecosystem stability.

stabilizing the ball on the peak has less to do with the magnitude of force applied and more to do with the type of force. For example, forests that are quite resilient in the face of the enormous destructive power of catastrophic fire may be degraded by herbiciding early successional nitrogen-fixing plants.

2. While one generally gets some warning that a ball in a well is being pushed toward the edge of stability, the ball on the peak already exists on the edge; hence, it is subject to rapid change with little advance warning.

The ball-on-the-peak stability of ecosystems — indeed, of any complex system — is qualitatively the same kind of balanced disequilibrium that is exhibited by a dancer in arabesque or Michael Jordan during a slam dunk. Disequilibrium with local environments results largely from feedbacks within the system — especially positive feedbacks such as those between plants and soils and plants and pollinators (DeAngelis et al. 1986; DeAngelis & Waterhouse 1987; Pastor & Post 1988; Perry et al. 1989b). But strong positive feedback within a system is also an Achilles' heel. Once started in the wrong direction, positive feedback rapidly tips the ball off the peak, whence it falls into an equilibrium state such as that exhibited by the clearcut at Cedar Camp.

Natural ecosystems maintain a balanced, stable disequilibrium through the buffering capacity of biodiversity (Perry et al. 1989b). In the forests of southwest Oregon and northern California, for example, a variety of tree and shrub species with differing adaptations to fire are capable of stabilizing the belowground ecosystem following disturbance. This redundancy, which in ecological jargon amounts to a diffuse mutualism, min-

imizes the chances that the plant-soil links will be severed and the system degraded by the inevitable disturbances of its environment.

Species Migrations, Ecosystem Stability, and Soils

Consider two hypothetical situations. In the first, the belowground communities supported by outgoing plants meet the needs of immigrants, and there is sufficient overlap between the two to stabilize the belowground, resulting in a smooth transition. In the second, overlap between compatible plants is insufficient to stabilize the belowground, nonmycorrhizal weeds capture the site, and soils begin to lose critical organisms, nutrients, and structure. The longer sites are without trees (or other plants that do equivalent things in the soil), the more difficulty migrating tree species will have in getting established; positive feedback drives the site further and further from reforestability.

How specific is the relation between particular plant species and mycorrhizal fungi and soil microbes? Can we predict the compatibility of the belowground of residents and the needs of immigrants? VAM fungi are believed to be quite general in their host preferences, and most EM fungi are known to form mycorrhizae with at least several different plant species. However, much research is needed on the host ranges of both fungal types. For example, though traditionally believed to form symbioses only with woody plants, EM have recently been reported on herbs and grasses (Kope & Warcup 1986; Trappe 1988; Warcup 1988). Except for the nodule-forming nitrogen-fixers (*Rhizobium* sp. and *Frankia* sp.), rhizobacteria are probably generalists; however, we are aware of no work that addresses this point.

EM and VAM trees commonly occur together in temperate and some tropical forests, but within each of these broad groups (EM or VAM) we might predict that plant species occurring together within a given community or occupying different seral stages on the same site support at least some of the same mycorrhizal species and probably many of the same rhizobacteria as well. In the Siskiyou mountains of southwest Oregon and northern California, for example, species in six families form EM, and we know that at least some of the hundreds of EM fungal species in these forests are shared by conifers and hardwoods (Borchers & Perry 1990). In the Siskiyou, hardwood trees and shrubs that occur in mixed communities with conifers impose patterns on soils that greatly benefit conifer growth (Amaranthus & Perry 1989; Borchers & Perry 1990; Amaranthus et al. 1990). Whether this is due to shared mycorrhizal fungi or something else remains to be determined, but the effect appears to be primarily biotic rather than abiotic. Compared to seedlings grown in soils previously occupied by grasses and herbs, conifer seedlings grown in soils previously occupied by associated hardwoods form root

tips faster following planting out, form more total as well as different types of mycorrhizae, and support higher levels of nitrogen-fixing bacteria in their rhizospheres. So far we have found these soil-mediated benefits only between species that grow together in mixed stands. Soils beneath Oregon white oak (*Quercus garyanna*), an EM tree that grows in single-species stands within the Siskiyou, do not benefit conifer growth.

Other recent studies show that mycorrhizal fungi can convert a negative interaction between individuals of two different plant species into one that is either neutral or positive. Puga (1985) demonstrated that while two VAM plant species (maize and a tropical weed) mutually inhibited one another when nonmycorrhizal, when mycorrhizal the two actually enhanced one another's growth. We have seen a similar phenomenon with EM trees. When grown together in pots without being inoculated with mycorrhizal fungi, Douglas-fir and ponderosa pine mutually inhibit one another's growth. This does not occur, however, with mycorrhiza-inoculated seedlings (Perry et al. 1989a). The similar responses seen in these two experiments, conducted with two widely different sets of plant species, suggest that mycorrhizal mediation of plant competition might be widespread in nature. One possible mechanism for this is that the fungi link the plants and facilitate a more even distribution of resources (Perry et al. 1989a). Considerable research shows that carbon and nutrients move from one mycorrhizal plant species to another, presumably through hyphal links (Brownlee et al. 1983; Read et al. 1985; Finlay & Read 1986a, b; Francis et al. 1986).

Implications for Migration

Based on the evidence reviewed above we hypothesize that immigration of a given plant species onto a new site will be facilitated (at least from a soils standpoint) if the immigrant and at least some of the species currently resident on that site occur together elsewhere. Many dry forests in northern California and southern Oregon, for example, comprise mixed communities of Douglas-fir, ponderosa pine, and a variety of EM hardwood trees and shrubs. Douglas-fir also extends northward on relatively mesic sites throughout the Pacific Northwest. Providing there is sufficient overlap between immigrants and emigrants, drought-tolerant ponderosa pine and hardwoods moving north into Douglas-fir forests should find a receptive soil ecosystem that reduces competition between resident Douglas-fir and newcomers. Similar arguments can be made for the movement of Douglas-fir up in elevation onto sites formerly held by true firs (*Abies* sp.). On the other hand, movement of rangeland plants (predominantly VAM) up in elevation onto sites dominated by EM trees could be inhibited by lack of VAM fungi. Kovacik et al. (1984) found no VAM fungal spores in soils beneath living ponderosa pine

trees. In the northeastern United States and upper Midwest, EM hardwoods may establish more readily than VAM hardwoods on former conifer sites of the boreal zone. Of course many factors other than soil receptivity will come into play to influence migration patterns.

Some fungal species may migrate along with their hosts, but many will not. All VAM fungi and an important subset of EM fungi fruit belowground and hence spread slowly. Many EM fungi fruit aboveground and are probably widely disseminated; however, studies of unreforested clearcuts show that spore rain does not maintain the MIP of soils on sites where host plants are absent (Perry et al. 1987). More work is needed on this point, but the mycorrhizal inoculation potential (MIP) of soils may drop rapidly in the absence of host plants. Jasper et al. (1989) found that the MIP of VAM fungi declined sharply within three weeks of clearing vegetation. Virtually all studies show that seedlings form the most mycorrhizae and form them most rapidly when their roots are in contact with mycorrhizal roots of an already established plant (Read 1988; Amaranthus & Perry 1989; Amaranthus et al. 1990).

Implications for System Stability During Changing Climates

The arguments presented above have at least two implications for species movements and ecosystem stability in the coming decades. First, although the pollen record suggests that plant species have migrated separately during historic climate changes (Hunter et al. 1988), it does not follow that they migrate independently of one another. The migrating plant moves within a milieu of interaction with other plants of the same and different species, its success on any given site conditioned — and probably ultimately determined — by the plant species that are already there, whether they be long-time residents or recently established newcomers. Competition between residents and immigrants has been considered (Brubacker 1986); cooperation, mediated through common interests in the health of the soil ecosystem, must also be considered. It is in fact the independent responses of plant species to environmental factors that buffer and stabilize the belowground of a given community against the fluctuations in climate and disturbance that are inevitable in nature. Serendipitously, two facts — that plant species with different environment adaptations share belowground mutualists, and that differing ranges of various plant species occur within a given region — should provide highways of migration to smooth those aspects of transition that are mediated by the physical and biological attributes of the soil.

A second implication relates to ecosystem stability during the transition from one community type to an-

other. We have argued that a smooth transition will require a certain amount of temporal overlap between residents and those immigrants that will contribute to maintaining nonequilibrium aspects of soil biology, structure, and nutrient cycling. Will the ball stay on the peak long enough for immigrants to arrive and establish or will it tip off and open the site to weeds? The answer to this question will require much more knowledge. How much overlap is enough? What is the time frame of soil deterioration? What plant species stabilize which parts of the soil? What plant species are "weeds" in the sense we use here — that is, that invest little energy in belowground processes? Again, the fact that plant species with differing environmental tolerances share belowground mutualists is a potentially important factor influencing the response of systems to changing climate. A relatively drought-intolerant species, for example, may resist a drying climate more successfully if it shares mycorrhizal fungi with a more drought-tolerant species within the same community (as is the case in forests of southern Oregon and northern California).

Although predicted rates of climate change are likely to exceed the dispersal ability of most or all trees and shrubs, the buffering capacity of healthy forests and rangelands may enable them to resist changes long enough to allow immigrants to establish a foothold and take over the job of stabilizing the soil (c.f. Brubaker 1986; Payette et al. 1990). The problem with this scenario is that many of our forests and rangelands are not healthy. Pollution and chronic insect infestations have already weakened forests of Europe and eastern North America, and exotic weeds such as *Bromus tectorum* have a strong foothold throughout the rangelands of western North America. Unless we take immediate measures to restore these systems to the original plant communities, and then protect these communities by sharply curtailing pollution and carefully reevaluating what constitutes a sustainable level of grazing, climate change may well apply the coup de grace to the plant-soil links.

Increased insect and fire activity associated with warmer, drier conditions (e.g., Overpeck et al. 1990) will reduce the capacity of forests to maintain healthy soils during community transitions. In at least some circumstances this problem is likely to be exacerbated by common management practices such as clearcutting and killing early successional shrubs and trees that have no commercial value. Seedling establishment in cleared areas is a potentially stressful period under the best of conditions, and a time in which the plant-soil links are especially vulnerable. The most prudent management course under the conditions we are now facing is to protect the soil by maintaining a cover of vigorous trees and/or shrubs at all times. This argument can be extended to agriculture, where stabilization of soil structure and biology with the right kind of green cover

crops could enhance the ability of agroecosystems to resist drought and other stresses associated with changing climates. The extent of soil change possible under fallow should not be underestimated. One study showed that 80 percent of large soil aggregates were lost within one year after converting a perennial grassland to fallow (Low 1955). Recovery of soil structure after plants were reestablished took much longer.

Fire susceptibility will be a particular concern in forests that experience warmer and drier climates. Although patterns may be quite different elsewhere, in the Pacific Northwest old-growth forests are more resistant to catastrophic fire than young to middle-aged forests (Perry 1988). Moreover, experience during the large wildfires of 1987 in Oregon and California indicates that some species of hardwoods act as heat sinks (their foliage desiccates but does not flame); hence, they actually protect admixed conifers during fires. These patterns further argue against clearcutting and excessive vegetation management in the coming decades. On the other hand, in some forest types old growth is the most susceptible to catastrophic fire (e.g., the northern Rockies; Romme & Despain 1989). One recipe is unlikely to serve all; however we must begin now to learn more about how species composition and stand structure influence the flammability of all our forest types.

We close by reiterating that, while the basic arguments presented herein are supported by evidence, much more study will be necessary to predict how the ecological interactions that we discuss will play out at any one place on the ground. In the legitimate haste of the scientific community to understand the large-scale atmospheric phenomena associated with climate change, we should not forget that part of the equation that deals with the ecological changes occurring in local ecosystems. It is the sum of these acting in concert with the atmosphere and oceans that will determine our future.

Despite the paucity of detailed knowledge concerning interactions between plants and soil, it seems clear that the integrity of most of the world's plant communities is intimately intertwined with that of the soils upon which they rely. Moreover, the evidence to date suggests that a shared interest in the continuing health of the soil acts through evolutionary time to forge links of cooperation among diverse plant species. Exactly how these interrelationships might influence the integrity of ecosystems during changing climates is unclear, but there is little doubt that they will play a role.

Acknowledgments

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